

Juvenile growth and survival under dietary restriction: are males and females equal?

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The effects of food availability on life-history traits may be direct or delayed and may vary between the sexes. We evaluated the effects of dietary restriction early in life on growth and survival of male and female juveniles in the common lizard (*Lacerta vivipara*) and surveyed the literature on sex-specific sensitivity to the environment in vertebrates. Juvenile lizards were reared in the laboratory during one month following birth under full feeding or under dietary restriction. They were then released in two outdoor enclosures, where we compared growth and survival between treatments during one year. Low food availability early in life led to lower body growth in a direct, but not delayed, manner. The absence of compensatory growth in juveniles that experienced dietary restriction might be explained by their reduced competitiveness. Dietary restriction had a strongly negative, delayed effect on survival up to the age of one year that was mediated by selection against smaller individuals. Effects of dietary restriction were not sex-specific, as expected from the similar energetic requirements of male and female juveniles. Hence, food availability has long-lasting consequences on life-history traits that might influence population dynamics in this species.

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Resource intake and allocation early in life are critical determinants of life-history traits in natural populations (van Noordwijk and de Jong 1986, Metcalfe and Monaghan 2001). Food availability can influence growth, maturation or reproduction in a direct way, suggesting that food intake may constrain lifetime reproductive success in the wild (Martin 1987). For example, a rich diet is often associated with faster growth, earlier maturation and larger asymptotic body size (Stamps 1993). A shortage of food early in life can also have more subtle long-term consequences, involving delayed effects on life-history traits. Individual performances throughout life might be strongly diminished by early dietary restriction. On the contrary, individuals

might be able to compensate for a bad start by growing faster later in their life (Madsen and Shine 2000, Metcalfe and Monaghan 2001). However, relatively few studies have investigated both direct and delayed consequences of early nutrition on life-history traits in vertebrates (de Kogel 1997, Madsen and Shine 2000).

Sex can have a major influence on the extent to which food availability affects life-history traits. For instance, larger body mass in one sex is often caused by faster growth, entailing that the larger sex requires more energy (Trivers 1972). Sexual dimorphism in body mass can thus lead to sexual differences in susceptibility to dietary restriction during ontogeny because of the energetic costs associated with faster growth (Fiala and Congdon

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1983, Clutton-Brock et al. 1985, Moore and Wilson 2002). Several field studies indeed found that life-history traits are more sensitive to dietary restriction in the larger than in the smaller sex (Tschirren et al. 2003). A higher susceptibility to dietary restriction in males could however also be the consequence of immunosuppressive effects of high testosterone levels (Grossman 1985, Zuk 1990). Furthermore, susceptibility to dietary restriction may be stronger in the heterogametic sex because of deleterious sex-linked mutations (Trivers 1972). Here, we study the direct and delayed consequences of early dietary restriction on growth and survival in juvenile common lizards (*Lacerta vivipara* Jacquin), and investigate sexual differences in direct and delayed susceptibility to dietary restriction.

The common lizard is an appropriate model for such a study. The species is widely distributed in Eurasia and exhibits considerable variation in life-history traits among natural populations (Lorenzon et al. 2001). The hypothesis that food availability may contribute to this variation is supported by the findings of significant natural variation in food availability (Khodadoost et al. 1987) and of strong competition for food in the wild (Massot et al. 1992). Furthermore, the common lizard is a short-lived species with continuous growth in which food availability early in life is likely to be a strong influence on growth rates, hence age at first reproduction and fecundity (Lorenzon et al. 2001). Finally, the experimental study of sex-specific sensitivity to early dietary restriction was facilitated by previous investigations of food requirements in this species (Avery 1971).

In order to understand the direct and delayed consequences of early dietary restriction on male and female common lizards, we manipulated food availability in the laboratory during the first month of life and next released the lizards in two outdoor enclosures where individual growth and survival were measured until the age of one year. To test the hypothesis that mass dimorphism between the sexes predicts which sex would be more affected by dietary restriction, we complemented this one-year manipulative study with monitoring of sexual dimorphism and sexual differences in juvenile survival in non-manipulated outdoor enclosures over three successive field seasons. The use of this unmanipulated group also allowed us to study sex-specific juvenile growth and survival for a longer period than the one of the manipulative study. We contrast our results with the general pattern observed in vertebrates

by reviewing previous experimental investigations of sex-specific environmental sensitivity.

Material and methods

Manipulation of food availability

The common lizard feeds upon a wide spectrum of small invertebrates (Avery 1971). In summer 2002, we manipulated the quantity of a prey species (larvae of the cricket *Acheta domestica*) with which offspring lizards (marked by toe clipping) were fed in the laboratory until the age of one month. Food treatments were designed on the basis of growth data obtained from the field study of Le Galliard et al. (2003) and of physiological data reported by Avery (1971) (Table 1). A distribution of individual growth rates under natural conditions was calculated using the field data. The physiological data of Avery (1971, section d) were used to convert these growth rates into food consumption rates. The average high food treatment (HF) was chosen as 61.5 mg per day, which corresponds to full feeding compared to levels observed in the field (Le Galliard et al. 2004). The average low food treatment (LF, 20.5 mg day⁻¹) was defined as one third of the high food level, corresponding to dietary restriction. The prey stock was obtained from Kreca Inc. (Ermelo, Holland), and prey items were counted and weighted each day prior to feeding.

Juvenile lizards were obtained from gravid females captured in July 2002 in a natural population (Mont Lozère, 44°27'N, 3°44'E). The mean clutch size was 5.55 ± 1.39 SD (range: 1–10) and all clutches were produced during five consecutive days, thus minimising the effects of timing of birth. Offspring sex was determined by counting ventral scales (Lecomte et al. 1992). We then randomly selected two sons and two daughters per clutch in 32 clutches (n = 128 juveniles). Juveniles' body length (from snout to vent), tail length (from vent to tip of tail) and body mass were measured to the nearest mm and mg. One sibling of each sex was assigned randomly to a low or a high food treatment. Lizards were then kept in individual terrariums (17 × 11 × 12 cm) and pooled in groups of four siblings under the same heating lamp. Siblings' groups were distributed on shelves according to a randomised block design, each block consisting of a tray with three heating lamps. Food manipulation was initiated at the age of four days and lasted four weeks. Terrarium substrate was made of

Table 1. Food delivery (mg day⁻¹ of house crickets larvae) per lizard during the period of the food manipulation (from 4 to 31 days of age). The weekly change was calculated to match the increasing energetic requirements of growing individuals.

	1st week	2nd week	3rd week	4th week	Average
Low food	15	17	21	29	20.5
High food	45	51	63	87	61.5

heath soil and high humidity was maintained along with permanent access to water and an optimal thermal gradient (19–20°C to 35–37°C). UV light was provided every other day (Iguana Light 5.0 UV-B, ZooMed, 40 W) to facilitate vitamin D metabolism and calcium uptake. The same person measured body length, tail length and body mass once per week. At the same time, remaining crickets were counted and removed. The proportion of crickets consumed was independent of sex ($\chi^2=0.65$, 1 df, $P=0.42$), but was affected by treatment ($\chi^2=6.23$, 1 df, $P=0.01$). The difference in proportion eaten between LF (99.5%) and HF (97.8%) treatments was however small, reflecting feeding close to satiety in the HF group.

Only one female from the low food treatment died during the laboratory study (on the last day). All other juveniles were released after the last measurement (from the 25 to the 30 August 2002) and families were distributed between two 10 × 10 m square outdoor enclosures along with 13 adults and 30 yearlings. Enclosures were located 100 m apart in the same meadow at the Ecological Research Station of Foljuif (48°17'N, 2°41'E). Individuals were recaptured and measured for length and mass. Captures were done twice before wintering, on the 11 and 25 September 2002 (censuses 1 and 2) and twice after wintering, on the 7 April and 26 May 2003 (censuses 3 and 4). All individuals were removed from the enclosures after May 26. This protocol was chosen to simulate competition between fully fed and food restricted individuals. Such competition can be expected in natural populations due to local variations in food availability and dispersal of offspring in the few weeks following birth (Massot and Clobert 1995).

Sexual differences in morphology and survival in unmanipulated juveniles

Using an independent data set, sexual differences in morphology and survival of unmanipulated juvenile lizards were measured in 1999, 2000 and 2001 in outdoor enclosures at the Ecological Research Station (Le Galliard et al. 2003). All of 1312 neonates from 263 families were measured for body length, tail length and body mass at birth. Individuals were released in similar outdoor enclosures one day after birth. Permanent access to a wide range of natural preys was provided in the outdoor enclosures (Boudjemadi et al. 1999) and food availability in enclosures was similar to the diet in the HF group of manipulated juveniles (Le Galliard et al. 2004). Individuals were measured again for body length, tail length and body mass when recaptured at the average age of 27.7 days (± 9.16 SD). This recapture session was aimed at estimating growth rates during the same period as in our laboratory study. Unmanipulated

juveniles have similar growth rates as manipulated juveniles from the HF group (Le Galliard et al. 2004). All individuals were released again and recaptured at the approximate age of 10 months, in late May of each year following birth (capture probability >0.9). This recapture session was aimed at measuring annual survival probabilities. Unmanipulated juveniles survived better than manipulated juveniles, which probably reflects a cost of moving manipulated juveniles from the laboratory to the outdoor enclosures at the age of one month (Le Galliard et al. 2004).

Statistical analyses

We used mixed-effects linear models to study the consequences of food availability on growth, and the sexual dimorphism at birth and during the first month of life observed in unmanipulated juveniles. We analysed body length, tail length and body condition (body mass adjusted for body length using residual scores of a linear regression). When studying the effects of food availability on morphology, sex, food treatment and their interaction were treated as fixed factors, while block (position in the laboratory) and sibship (categorical variable with one level per family) were included as random effects. When studying the sexual dimorphism at birth and during the first month of life in unmanipulated juveniles, sex, year and their interaction were treated as fixed factors, while sibship nested within each year was included as random factors. Because growth rates decrease with size in species with indefinite growth such as the common lizard (Stamps 1993), the initial value of each morphological trait was used as a covariate in all models. Parameters were estimated with the procedure MIXED in SAS (Littell et al. 1996) and random effects were tested with likelihood ratios (Stram and Lee 1994). Results are given as means \pm SE.

We analysed survival probability from birth to the age of ten months with mixed-effects logistic regressions. Survival after the food manipulation was modelled with food treatment, sex, morphology at release, enclosure and their interactions as fixed factors, while sibship within each enclosure was included as a random effect. We also modelled survival during the three-years long field survey of unmanipulated juveniles by including sex, year and their interaction as fixed factors and the random effect of sibship nested within each year. Parameters of these models were estimated with the GLIMMIX macro in SAS (Littell et al. 1996). We further analysed the recapture data set of our food manipulation with a Cormack-Jolly-Seber model describing capture and survival probabilities (Lebreton et al. 1992, White and Burnham 1999). Sex, food treatment and census period were treated as factors

affecting both capture and survival probabilities. The full model involved these factors and their interactions, as well as an effect of enclosure and an interaction between enclosure and census period. Capture probability during the last census was fixed to one. The goodness-of-fit of the full model was tested with a parametric bootstrap (1000 simulations, Anderson and Burnham 1994). We next applied backward elimination based on likelihood ratio tests to select a model describing capture probabilities and then selected a model describing survival probabilities (Lebreton et al. 1992).

Results

Direct effects of diet on morphology

Dietary restriction had a direct, negative effect on growth rates in the laboratory (Table 2). The three-fold decrease in food availability resulted approximately in a three-fold decrease in growth rates for body and tail length (Fig. 1). Sexual differences between juveniles were significant for growth in body length and body condition, but not for tail length (Table 2). Body length grew more rapidly in females (females: $5.05 \text{ mm} \pm 0.14$, $n = 64$; males: $4.46 \text{ mm} \pm 0.14$, $n = 64$), whereas body condition increased more in males (contrast = 0.033 ± 0.008). Dietary restriction had similar effects in males and females (Fig. 1, Table 2).

To test if different families responded similarly to dietary restriction, we included an interaction between the sibship effect and the food treatment effects in the models presented in Table 2. We found that plastic changes in growth in response to food availability were not different among families in the case of body length, tail length or body condition (χ^2 tests, all $P > 0.10$). This result is well illustrated by the parallelism of the familial reaction norms to food availability (body size in Fig. 2).

Delayed effects of diet on morphology

Delayed effects of food treatment on growth were investigated from release to census 2. Release, census 1

and census 2 data were included in repeated-measures analyses of body length, tail length and body condition ($n = 57$ individuals). There was a strong effect of treatment on the three morphological traits (all $P < 0.0001$), but no significant interaction between food treatment and time, and between food treatment, time and sex (all $P > 0.60$).

Effects of diet on survival

Starting from the full Cormack-Jolly-Seber model, we assumed that survival probability from census 3 to census 4 was equal to one because all animals from census 3 were also seen in census 4. This model adequately fitted the data (GOF test, $P = 0.68$, estimated over-dispersion quasi-likelihood parameter = 0.75). Capture probability was not affected by census period, sex, enclosure or food treatment (likelihood ratio tests, all $P > 0.09$, mean capture probability = 0.891 [0.803, 0.942] 95% CI). Survival probability was affected by food treatment ($\chi^2 = 7.84$, 1 df, $P = 0.005$), time ($\chi^2 = 7.74$, 2 df, $P = 0.02$) and an interaction between time and enclosure ($\chi^2 = 7.48$, 2 df, $P = 0.02$). The latter was due to a lower survival during the wintering period in one enclosure. The effect of treatment on survival did not decay over time (food treatment \times census time: $\chi^2 = 1.31$, 2 df, $P = 0.52$), and the consequences of treatment were similar in males and females (food treatment \times sex: $\chi^2 = 1.37$, 1 df, $P = 0.24$, Fig. 3), irrespective of the period (food treatment \times sex \times time: $\chi^2 = 0.89$, 2 df, $P = 0.64$). Overall, the annual juvenile survival (obtained as the product of the survival probabilities reported in Fig. 3) was 0.25 (± 0.06 SE) in the HF group and 0.02 (± 0.01 SE) in the LF group. In the multiple logistic regression analysis of annual survival, body length was the only significant variable (odds ratio per mm body length = 0.52, $\chi^2 = 20.1$, 1 df, $P < 0.0001$). The effect of treatment on annual survival was not significant when body length was included as a covariate in the model ($\chi^2 = 0.02$, $P = 0.88$).

Table 2. Effects of food availability on growth rates of male and female lizards for body length, tail length and body condition. Boldfaced results indicate significant factors after a sequential Bonferroni correction. Two observations were excluded from the analyses of tail length and body condition because of tail loss during the study.

Factor	Body length	Tail length	Body condition
Value at birth	F_{1,92} = 29.70***	F_{1,90} = 17.30***	F_{1,90} = 4.63*
Food treatment	F_{1,92} = 902.70***	F_{1,90} = 771.80***	F_{1,90} = 18.20***
Sex	F_{1,92} = 8.96**	F _{1,90} = 0.46	F_{1,90} = 22.10***
Food treatment \times sex	F _{1,92} = 0.20	F _{1,90} = 0.05	F _{1,90} = 0.24
Block		No variance among blocks	
Sibship(block)	$\chi^2 = 1.10$	$\chi^2 = 12.10**$	$\chi^2 = 4.20*$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

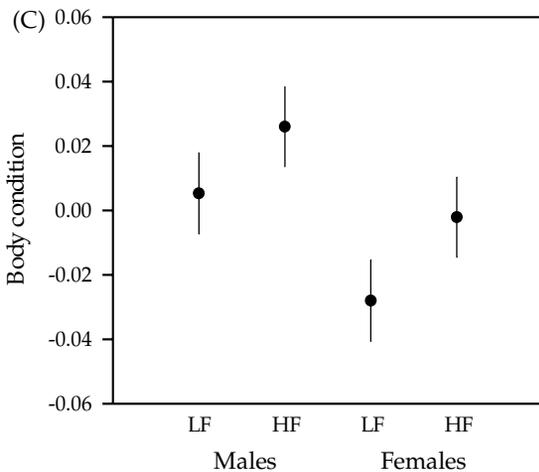
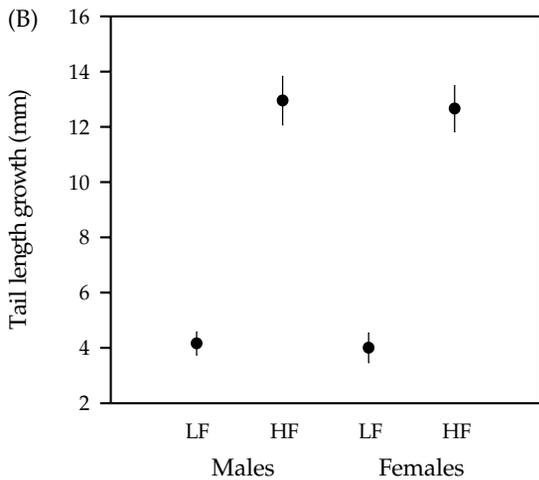
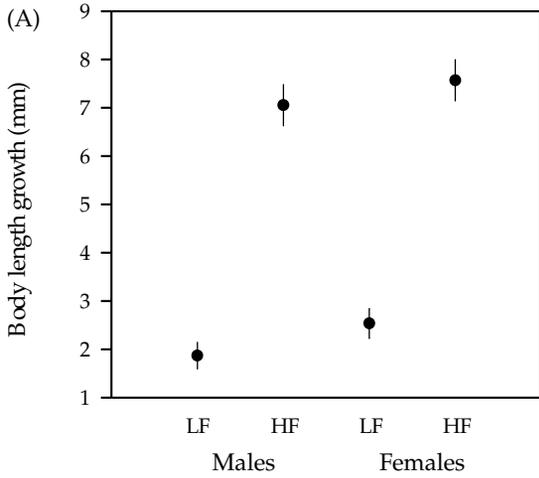


Fig. 1. Effect of food availability on growth of male and female lizards. Data are given as means (± 2 SE) per sex and treatment. LF: low food treatment. HF: high food treatment. Sex-specific growth from birth to the age of one month is shown for body length (from snout to vent, (A), tail length (B)) and body condition (body mass adjusted for body length, (C)).

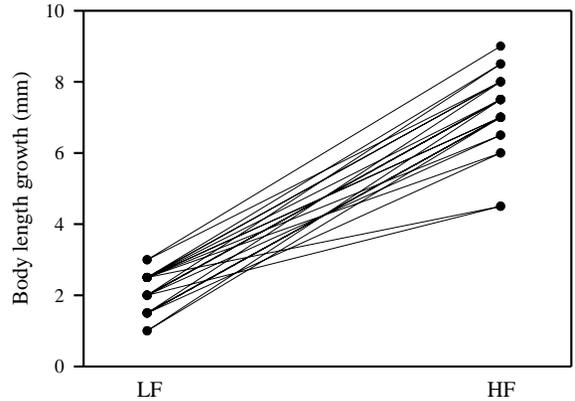


Fig. 2. Familial reaction norms of growth in body length (from snout to vent) in response to food availability. Data are given as mean growth from birth to the age of one month per family and treatment. LF: low food treatment. HF: high food treatment. There was no significant interfamily variation in the sensitivity of growth to food availability ($\chi^2 = 0.5$, $P = 0.48$).

Sexual differences in morphology and survival in unmanipulated juveniles

The general pattern of sexual differences in morphology and survival of unmanipulated juvenile lizards was assessed using an independent data set collected in 1999, 2000 and 2001. During these three years, body mass at birth and growth in body mass did not differ between the sexes ($F_{1,1047} = 1.88$, $P = 0.17$ and $F_{1,582} = 0.10$, $P = 0.76$, respectively). Body length, tail length and body condition at birth differed between sexes (Table 3). Females had a higher body length at birth than males (females: $23.2 \text{ mm} \pm 0.08$, $n = 610$; males: $22.4 \text{ mm} \pm$

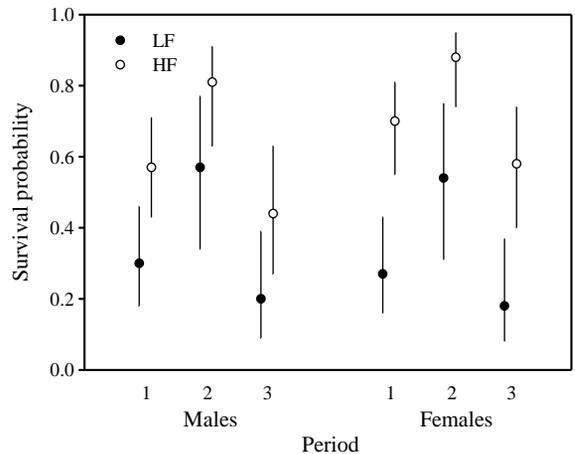


Fig. 3. Effect of food availability on survival in male and female lizards. Data are mean survival probabilities (95% CI) per sex and per period. Survival probabilities were estimated with a mark-recapture model involving constant capture effort (see text for explanations). LF: low food treatment. HF: high food treatment. Period 1: from release to census 1. Period 2: from census 1 to 2. Period 3: from census 2 to 3.

Table 3. Sexual dimorphism at birth and during ontogeny for body length, tail length and body condition in unmanipulated juveniles. Body condition at birth was analysed with an ANCOVA involving body mass as a response and body length as a covariate. Boldfaced results indicate significant effects after sequential Bonferroni correction.

Response	Factor	Body length	Tail length	Body condition
Value at birth	sex	$F_{1,1048} = \mathbf{350.7^{***}}$	$F_{1,1048} = \mathbf{41.3^{***}}$	$F_{1,1047} = \mathbf{68.1^{***}}$
	year	$F_{2,260} = \mathbf{22.7^{***}}$	$F_{2,260} = \mathbf{10.1^{***}}$	$F_{2,260} = \mathbf{26.5^{***}}$
	sibship(year)	$\chi^2 = \mathbf{632.2^{***}}$	$\chi^2 = \mathbf{536^{***}}$	$\chi^2 = \mathbf{939^{***}}$
Growth rates	value at birth	$F_{1,584} = \mathbf{8.0^{**}}$	$F_{1,584} = \mathbf{4.1^*}$	$F_{1,582} = \mathbf{368.9^{***}}$
	sex	$F_{1,584} = 3.04^\dagger$	$F_{1,584} = 0.2$	$F_{1,582} = \mathbf{87.4^{***}}$
	year	$F_{2,233} = \mathbf{6.47^{***}}$	$F_{2,233} = \mathbf{39.6^{***}}$	$F_{2,233} = \mathbf{119.7^{***}}$
	sibship(year)	$\chi^2 = \mathbf{364.5^{***}}$	$\chi^2 = \mathbf{78.9^{***}}$	$\chi^2 = \mathbf{8.2^{**}}$

$^\dagger P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

0.08, $n = 702$), a shorter tail (females: $22.5 \text{ mm} \pm 0.15$; males: $23.1 \text{ mm} \pm 0.15$), and a lower body condition (body mass adjusted for body length, females: $188 \text{ mg} \pm 1.6$; males: $194 \text{ mg} \pm 1.6$). Variation in body condition was influenced by sex, whereas sexual differences in body size growth were only marginally significant (Table 3). Males gained more body condition compared to females (contrast = 0.003 ± 0.00035) while females tended to grow to longer size than males.

Survival probability from birth to the age of one year was changed by accidental invasion by greater white-toothed shrews (*Crocodyrus russula*) in five enclosures in 1999 and in one enclosure in 2001 (Le Galliard et al. 2003). When comparing juveniles from invaded and non-invaded enclosures in 1999 (1446 juveniles from 282 families), we found that white-toothed shrews affected juvenile survival ($\chi^2 = 14.29$, 1 df, $P = 0.002$) independent of juvenile's sex ($\chi^2 = 1.90$, 1 df, $P = 0.17$). Invasion of an enclosure by shrews reduced annual juvenile survival from 0.29 (± 0.04) to 0.07 (± 0.03) in 1999. With data from the enclosures invaded by shrews removed, we analysed differences in survival probabilities between sexes during three years (1059 juveniles from 229 families). The average survival probability was 0.42 (± 0.03 SE) for male and 0.39 (± 0.03) for female juveniles. The interaction between year and sex effects had no influence on survival ($\chi^2 = 2.95$, 2 df, $P = 0.23$), and there was no difference in survival probability between years ($\chi^2 = 3.23$, 2 df, $P = 0.20$) and sexes ($\chi^2 = 1.29$, 1 df, $P = 0.26$).

Discussion

Effects of food availability on growth and survival

Food availability varies among populations of the common lizard and may contribute to the spatial variations of life-history traits in this species (Khodadoost et al. 1987). Our experiment shows indeed that early food availability is a critical determinant of growth and survival in juveniles. We found strong evidences for a plastic increase in growth rates under a full feeding

regime. Such a dependence of growth on energy intake was known from earlier studies: effects of diet on morphology have already been demonstrated in some lizards (Dunham 1978, Stamps and Tanaka 1981) and also repeatedly in other taxa (Badyaev 2002). More interestingly, we found no catching-up in growth after dietary restriction was imposed early in life: fully fed juveniles maintained a larger body size in the field than dietarily restricted juveniles. Thus, growth was affected by early food availability in a direct, but not delayed, manner (Madsen and Shine 2000). The weak facility for rapid compensatory growth in juveniles undergoing dietary restriction could be due to their smaller size, making them uncompetitive against fully fed individuals.

Early food availability also had strong, delayed effects on survival: survival was lower in response to early dietary restriction and the consequences of early dietary restriction persisted during a period of approximately nine months. If body size is an important determinant of competitiveness in the field (Ferguson and Fox 1984), effects of early food availability on survival may be mediated by size-dependent survival in juveniles. This explanation was supported by the positive correlation between survival and body length upon release, and by the absence of treatment effect on size-independent survival. To our knowledge, this is the first experimental demonstration that food availability can influence survival in reptiles, and one of the few experiments showing a long lasting effect of diet on survival (Metcalf and Monaghan 2001). Our result is, however, at odds with the increased life span associated with food restriction in several experiments (Mair et al. 2003). As those experiments simulated competition within the same food treatment in the laboratory, we hypothesise that the lower survival of food restricted lizards in our study may be caused by maladaptive development due to under-nutrition or by the inferiority of food restricted individuals during competition with fully fed animals (Bateson et al. 2004). Altogether, the long-lasting consequences of early nutrition on body size and survival detected here will contribute to variations among cohorts within the same population and thus influence population dynamics in this species (Beckerman et al. 2002).

Sexual differences in sensitivity to dietary restriction

The effects of dietary restriction on growth and survival were similar in males and females, and we found no sexual differences in mortality neither in manipulated nor in unmanipulated juveniles. In both manipulated and unmanipulated juveniles, males and females were similar in body mass, even though sexes differed in body shape: body length was higher at birth and increased faster in females, tail length was higher at birth in males, and body condition was higher at birth and increased faster in males. Therefore, the sexual dimorphism observed in juvenile lizards resulted from a sex-biased pattern of allocation, but not acquisition, of resources, which suggests that sexes have similar energetic require-

ments across the juvenile stage. Our results, therefore, are consistent with the hypothesis that the absence of sex-specific susceptibility to dietary restriction is linked with the absence of sexual mass dimorphism (Clutton-Brock et al. 1985). Observations in agreement with ours have been obtained in two other vertebrate species where sexes have similar body mass (cf. references 5 and 10 in Table 4). In species characterised by sexual mass dimorphism, seven studies out of ten found that harsher conditions were more detrimental to the heavier sex (Table 4). However, it was impossible to distinguish the costs of being large from the costs of being a male in these studies because males were consistently the larger sex. The lack of sex differences in species that are

Table 4. Experimental studies on sex-specific environmental sensitivity in vertebrates. SMD = sexual mass dimorphism, CMD = cost of sexual mass dimorphism, CTM = cost of testosterone in males, CH = cost of heterogamety (see Introduction). Studies 3, 8–9 and 14 also suggested that the larger sex dominates the smaller sex during sibling competition in a poor environment.

Environmental factor	Species	Life-history stage	Main results	SMD	Compatible with	Ref.
Competition	Red-winged blackbirds <i>Agelaius phoeniceus</i>	Nestlings	Higher mortality of males in enlarged broods	Males heavier	CMD, CTM	1
	Rook <i>Corvus frugiferus</i>	Nestlings	Higher mortality of males in male-biased broods	Males heavier	CMD, CTM	2
	Great tit <i>Parus major</i>	Fledglings	Higher male to female ratio in recruits from enlarged broods, no effect on sex-specific growth	Males heavier	CH	3
	Zebra finches <i>Taeniopygia guttata</i>	Fledglings	Females from larger broods are more likely to die after independence	No dimorphism	CH	4
	Collared flycatchers <i>Ficedula albicollis</i>	Nestlings	No effect on sex-specific growth or recruitment	No dimorphism	CMD	5
	Eurasian kestrels <i>Falco tinnunculus</i>	Fledglings	Stronger decrease in cell-mediated immunity in males after brood size increase, no effect on sex-specific survival	Males heavier	CTM	6
Food availability	Wood rat <i>Neotoma floridana</i>	Lactation	Maternal dietary restriction during lactation affects male survival more than female survival	Males heavier	CMD, CTM, CH	7
	Golden hamster <i>Mesocricetus auratus</i>	Lactation	Maternal dietary restriction during lactation or early in life affects male survival more than female survival	Males heavier	CMD, CTM, CH	8–9
	Red squirrels <i>Tamiasciurus hudsonicus</i>	Before and shortly after weaning	No effect on sex-specific pre- and post-weaning survival	Males heavier after weaning	CMD	10
	Zebra finches <i>Taeniopygia guttata</i>	Nestlings	Low-quality maternal diet reduces female survival	No dimorphism	CH	11
	Lesser black-capped gull <i>Larus fuscus</i>	Nestlings	Maternal dietary restriction decreases survival of males but not females	Males heavier	CMD, CTM	12
	Tengmalm's owl <i>Aegolius funereus</i>	Nestlings	Male, but not female, survival diminishes due to dietary restriction in a poor year	Females heavier	CTM	13, 14
Parasitism	Soay sheep <i>Ovis aries</i>	Yearlings	Removal of gut parasites reversed the natural male-biased mortality	Males heavier	CMD, CTM, CH	15
	Great tit <i>Parus major</i>	Nestlings	Males growth reduced by hen fleas infection, no effect on sex-specific survival	Males heavier	CMD, CTM	16
Egg and parental condition	Great skua <i>Stercorarius skua</i>	Nestlings	No effect on sex-specific chick survival, but female-biased mortality	Females heavier	CMD	17

1. Cronmiller and Thompson 1981; 2. Røskaft and Slagsvold 1985; 3. Smith et al. 1989; 4. de Kogel 1997; 5. Sheldon et al. 1998; 6. Fargallo et al. 2002; 7. McClure 1981; 8. Huck et al. 1986; 9. Labov et al. 1986; 10. Boutin and Larsen 1993; 11. Bradbury and Blakey 1998; 12. Nager et al. 1999; 13. Hörnfeldt et al. 2000; 14. Hipkiss et al. 2002; 15. Gulland et al. 1993; 16. Tschirren et al. 2003; 17. Kalmbach et al. 2005.

monomorphic in mass, like the common lizard, lends weight to the view that sexual differences in susceptibility to environmental harshness are not due to sex per se. Nevertheless, experimental studies in species where females are larger than males are much warranted (Kalmbach et al. 2005). For example, females are usually heavier than males in raptors and two experimental studies found a stronger sensitivity of males to restricted food intake in these species (cf. references 6 and 13–14 in Table 4). Whether these latter results are due to costs of testosterone or to sibling competition for food favouring larger females remains however unknown (Fargallo et al. 2002).

Alternative to the effects of sexual mass dimorphism, males could be more sensitive to dietary restriction due to their early exposure to higher testosterone levels (Grossman 1985, Zuk 1990, Tschirren et al. 2003). Although testosterone levels in juvenile common lizards are not described, studies in the lizard *Anolis carolinensis* detected higher testosterone levels in the egg yolk and post-hatching plasma from male juveniles (Lovern et al. 2001, Lovern and Wade 2003). Our results do not agree with some deleterious effects of testosterone in juvenile males. However, testosterone effects can explain sexual differences in susceptibility to environmental harshness in nine studies out of the fourteen reviewed (Table 4). Studies that did not support this hypothesis, including our work, cannot rule out the alternative explanation that differences in testosterone levels between the sexes were absent or too weak to lead to significant sexual differences.

Our results oppose the hypothesis of deleterious effects of heterogamety in juvenile females. This hypothesis would predict a greater sensitivity to food deprivation in females, since the heterogametic sex is female in the common lizard (Chevalier et al. 1979). It has long been suggested that heterogamety does not explain patterns of male-biased mortality in birds and reptiles where the heterogametic sex is usually female (Clutton-Brock et al. 1985). Nevertheless, we reviewed two studies the results of which could only be explained by heterogamety (Table 4). In the first study (on great tits) measurements of survival might be have been biased by sex-specific movements out of the study area (Smith et al. 1989). In the second study (on captive zebra finches, cf. references 4 and 11 in Table 4), the cause of female biased mortality was questioned (de Kogel 1997) and the results were inconsistent with those of a previous study (Boag 1987). Therefore, we conclude that, in fact, these two cases provide weak evidence in favour of a cost of heterogamety in females.

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